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NEW MATERIAL AND PHYLOGENETIC POSITION OF *AIDACHAR PALUDALIS* NESOV, 1981 (ACTINOPTERYGII, ICHTHYODECTIFORMES) FROM THE LATE CRETACEOUS OF UZBEKISTAN

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ABSTRACT

Aidachar paludalis Nesov, 1981 from the Upper Cretaceous (Turonian) Bissekty Formation of Uzbekistan is referable to the teleost order Ichthyodectiformes by combination of the following diagnostic characters: large and massive intercalar, forming part of the hyomandibular facet and a canal for the jugular vein; deep premaxilla-maxilla attachment; deep dentary symphysis; angled coronoid process of the dentary; teeth forming a single series in the jaws. It shares a unique character with *Aidachar pankowskii* (Forey et Cavin, 2007), comb. nov., from the Cenomanian of Morocco: hyomandibular facet clearly divided into two parts.

Key words: *Aidachar*, Ichthyodectiformes, Late Cretaceous, Uzbekistan

НОВЫЙ МАТЕРИАЛ И ФИЛОГЕНЕТИЧЕСКОЕ ПОЛОЖЕНИЕ *AIDACHAR PALUDALIS* NESOV, 1981 (ACTINOPTERYGII, ICHTHYODECTIFORMES) ИЗ ПОЗДНЕГО МЕЛА УЗБЕКИСТАНА

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РЕЗЮМЕ

Aidachar paludalis Nesov, 1981 из верхнемеловой (турон) биссектинской свиты Узбекистана может быть отнесен к отряду костистых рыб Ichthyodectiformes на основании комбинации следующих признаков: большая и массивная вставочная кость, образующая часть гиомандибулярной фасетки и канал для яремной вены; высокое соединение предчелюстной и челюстной костей; высокий симфиз зубной кости; углообразный венечный отросток зубной кости; один ряд зубов на челюстях. Этот вид имеет уникальный признак, общий с *Aidachar pankowskii* (Forey et Cavin, 2007), comb. nov., из сеномана Марокко: гиомандибулярная фасетка ясно разделена на две части.

Ключевые слова: *Aidachar*, Ichthyodectiformes, поздний мел, Узбекистан

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INTRODUCTION

The extinct primitive teleost fishes of the order Ichthyodectiformes were common predators in the Mesozoic sea waters since the Middle Jurassic (Bardack 1965; Bardack and Sprinkle 1969; Patterson and Rosen 1977). Remains of some 20 genera and 40 species are found in North and South America, Europe, Asia, Africa, and Antarctica in predominantly marine deposits, while records of the group in the freshwater strata are quite rare (Patterson and Rosen 1977; Maisey 2000). This observation is apparently based on study of articulated fish skeletons. Disarticulated bones of ichthyodectiforms, mostly isolated teeth and vertebra, are common in microvertebrate samples from brackish to fresh water Late Cretaceous deposits of Kyzylkum Desert in Uzbekistan. Two taxa have been described by Nesov (1981a) based on jaw fragments: *Sultanuvaisia antiqua* Nesov, 1981 from the Cenomanian Khodzhakul Formation of South-West Kyzylkum Desert and *Aidachar paludalis* Nesov, 1981 from the Turonian Bissekty Formation of Central Kyzylkum Desert. These taxa were originally described as pterosaurs, but before that article was published, Lev Nesov realized that these remains are actually belonging to ichthyodectiform fishes (Nesov, personal communication to the second author in 1985). Later, Nesov (1985) cited the Cenomanian taxon as *Ichthyodectes antiquus* and described giant scales from the Bissekty Formation referred to ?Ichthyodectidae gen. et sp. nov. He mentioned also other remains of ichthyodectiform fishes from the Bissekty Formation, including a partial braincase found in 1980. This specimen was figured in Nesov (1997: pl. 6, fig. 7) where it was identified as a neurocranium of a teleost fish. Nesov (1997) figured but not described some other bones attributable to *Aidachar paludalis* from Uzbekistan, collected by him and his colleagues in 1977–1994. Abundant remains of ichthyodectiform fishes from the Bissekty Formation were also collected by Uzbek / Russian / British / American / Canadian Joint Paleontological Expedition in 1997– 2006 (abbreviated URBAC) (Archibald et al. 1998). Here we describe the most diagnostic specimens of *Aidachar paludalis* from the Bissekty Formation and discuss validity and phylogenetic relationships of this taxon.

Institutional abbreviations. CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; ZIN PC, Paleontological collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

SYSTEMATICS

Osteichthyes Huxley, 1880
Actinopterygii Klein, 1885
Teleostei Müller, 1845
Ichthyodectiformes Bardack et Sprinkle, 1969
Aidachar **Nesov, 1981**

Aidachar: Nesov 1981a, p. 99.

   Type species. *Aidachar paludalis* Nesov, 1981.
   Emended diagnosis. Differs form other ichthyodectiform genera by the hyomandibular facet clearly divided into two parts.
   Included species. Type species and *Aidachar pankowskii* Forey et Cavin, 2007, comb. nov., from the Cenomanian of Morocco.
   Comment. *Sultanuvaisia antiqua* Nesov, 1981 from the Cenomanian of Uzbekistan is known from jaw fragments, isolated teeth, and vertebrae. It is not clear if it is a distinct taxon or a synonym of *Aidachar paludalis* Nesov, 1981.
   Distribution. Late Cretaceous of North Africa and Middle Asia.

Aidachar paludalis **Nesov, 1981**
(Figs 1–7)

Pterosauria indet.: Nesov, 1981b, fig. 11–27.
Aidachar paludalis: Nesov 1981a, p. 100, fig. 1a–d; Nesov 1997, pl. 6, fig. 19.
Aidachar sp.: Nesov 1981a, fig. 1e–zh; Nesov 1997, pl. 6, fig. 16.
Ichthyodectidae? gen. et sp. nov.: Nesov, 1985, p. 206, pl. 2, fig. 8.
Ichthyodectidae indet.: Nesov 1986, fig. 1–11; Nesov and Udovichenko 1986, pl. 1, fig. 16; Nesov 1997, pl. 5, fig. 10, pl. 58, fig. 1.
Aidachar? sp.: Nesov 1997, pl. 6, fig. 6.
Ichthyodectidae? indet.: Nesov 1997, pl. 3, fig. 7, pl. 4, fig. 6, pl. 6, fig. 18.
Teleostei indet.: Nesov, 1997, pl. 6, fig. 7.

   Holotype. CCMGE 1/11913, left maxilla.
   Type locality and horizon. Dzharakuduk, Central Kyzylkum Desert, Uzbekistan; Bissekty Formation, Turonian, Upper Cretaceous.
   Material. ZIN PC 1/58, right premaxilla; ZIN PC 2, 5, and 7/58, right maxillary fragments; ZIN PC 3,
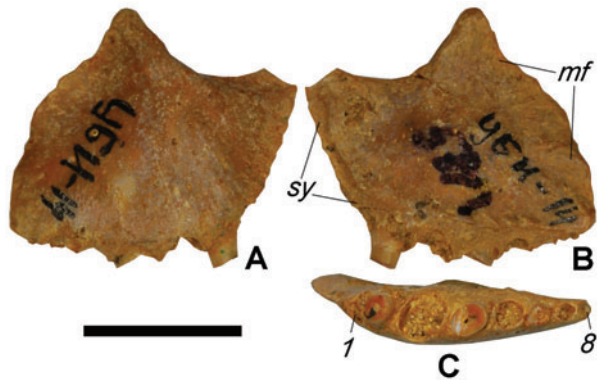
Fig. 1. *Aidachar paludalis*, right premaxilla (ZIN PC 1/58), in lateral (A), medial (B), and ventral (C) views; Dzharakuduk, Kyzylkum Desert, Uzbekistan; Bissekty Formation, Turonian, Upper Cretaceous. *Abbreviations*: *1* and *8* – first and eighth tooth positions; *mf* – maxillary facet; *sy* – symphysis. Scale bar = 10 mm.

4, 6, 8, and 9/58, left maxillary fragments; ZIN PC 14/58, partial braincase; ZIN PC 15/58, parasphenoid fragment with basipterygoid processes; CCMGE 5/12452, left dentary fragment. ZIN PC 16, 18, 19, 26, 27, and 37/58, left dentary fragments; ZIN PC 17, 21, 23–25, and 28–31/58, right dentary fragments; CCMGE 19–25/12000, jaw fragments; ZIN PC 38 and 39/58, isolated teeth; CCMGE 105/12177, abdominal vertebra; ZIN PC 40 and 41/58, abdominal vertebrae; CCMGE 18/12000, scale. Numerous not catalogued jaw fragments, isolated teeth, and vertebrae, and several scales. All specimens come from the type locality.

Description. The premaxilla is known from a single immature specimen (Fig. 1). It is a flattened rhomboid bone. The bone is higher than long. The dorsal margin is deeply incised. The symphysis is narrow and shorter than the dental margin. The pos-

Fig. 2. *Aidachar paludalis*, anterior fragments of left maxilla, ZIN PC 4/58 (A–D) and ZIN PC 5/58 (E–H), in dorsal (A, E), medial (B, F), lateral (C, G), and ventral (D, H) views; Dzharakuduk, Kyzylkum Desert, Uzbekistan; Bissekty Formation, Turonian, Upper Cretaceous. *Abbreviations*: *epf* – ethmopalatine facet; *pf* – palatine facet; *pmf* – premaxillary facet; *r*– ridge; *sg* –s upramaxillary groove. Scale bars = 10 mm.

Fig. 3. *Aidachar paludalis*, right maxillary fragment (ZIN PC 2/58), in dorsal (A), medial (B), lateral (C), and ventral (D) views; Dzharakuduk, Kyzylkum Desert, Uzbekistan; Bissekty Formation, Turonian, Upper Cretaceous. *Abbreviations: pf*– palatine facet; *r* – ridge; *sg* – supramaxillary groove. Scale bar = 10 mm.

terior margin is convex. On the medial side along the posterior margin there is a poorly differentiated maxillary facet. There are eight tooth positions; the teeth are present in the positions 2, 4, 6–8. The third tooth is the largest and the size of teeth decrease gradually from this position anteriorly and posteriorly.

The maxilla is represented by several mostly fragmentary specimens (Figs 2–3), including the holotype (Nesov 1981, fig. 1a–d; Nesov 1997, pl. 6: fig. 19). It is a long, dorsoventrally narrow and mediolaterally flat bone. The anterior end is bent medially at an angle of 20–25°. The anterior end of the bone is very thin and completely preserved only in ZIN PC 6/58 (Fig. 2E–F). A rugose area on its lateral surface apparently represents the articulation facet for the premaxilla. Along the dorsal margin, there are two similar well elaborated oval shaped articulation surfaces. The anterior and smaller facet is for articulation with the ethmopalatine. The posterior facet is for the palatine. Both facets are separated by a concavity along the maxillary dorsal margin.

The dorsal margin of maxilla is slightly sinusoid in lateral profile, with a concavity posterior to the palatine facet. It is flanked laterally by a distinct ridge, interrupted some distance posterior to the palatine facet (Figs 2A, 3A). Medial to this ridge, there is a distinct groove along the dorsal margin for the supramaxilla. The ventral margin of the bone is more sinusoid compared with the dorsal margin. There are two concavities along the bone length, the first of which is below and posterior to the palatine facet. The first dental alveoli are placed just at the posterior end of the premaxillary facet providing a continuous upper jaw tooth row. The first 10–11 teeth are small and located in a concave part of the maxillary ventral margin. The anterior convexity of the ventral margin bears the largest teeth and posteriorly the size of alveoli decreases more or less gradually.

ZIN PC 14/58 (Fig. 4) is an exquisitely preserved partial braincase. Its maximum length 86 mm and maximum width 76.8 mm. The fragment preserves variously complete parasphenoid, basioccipital, exoccipitals, intercalary, pterotic, prootic, and possible autosphenotic. The entire length of the neurocranium could be estimated as 160 mm based on proportions of neurocranium in *Ichthyodectes* (Bardack 1965, fig. 14).

The parasphenoid is incomplete, with the most of the part anterior to the basipterygoid process missing (Fig. 4A, C). The preserved portion of parasphenoid is arcuate, convex ventrally, with the maximum of curvature at the basipterygoid processes. The angle between orbital and otic portions of the bone is about 150°. Anterior to the basipterygoid processes the parasphenoid is triangular in cross section, with flattened ventral surface. Posterior to these processes the cross section of the bone is more rounded. The right basipterygoid process is nearly completely preserved. It is a stout laterally projecting process. The basipterygoid process is pierced by two canals both of which are directed dorsoanteriorly. The larger anterior canal is for the efferent pseudobranchial artery, the smaller and shorter canal is for the internal carotid artery. The canals for the internal carotid artery are better preserved in a parasphenoid fragment ZIN PC 15/58. The posterior part of the parasphenoid is forked and embraces the wedged anterior end of basioccipital. On the ventral side posterior to the basipterygoid processes, there is a longitudinal groove. This groove is diverging some distance before the basioccipital. There are several irregular foramina within or near this groove. Some of these foramina are apparently for
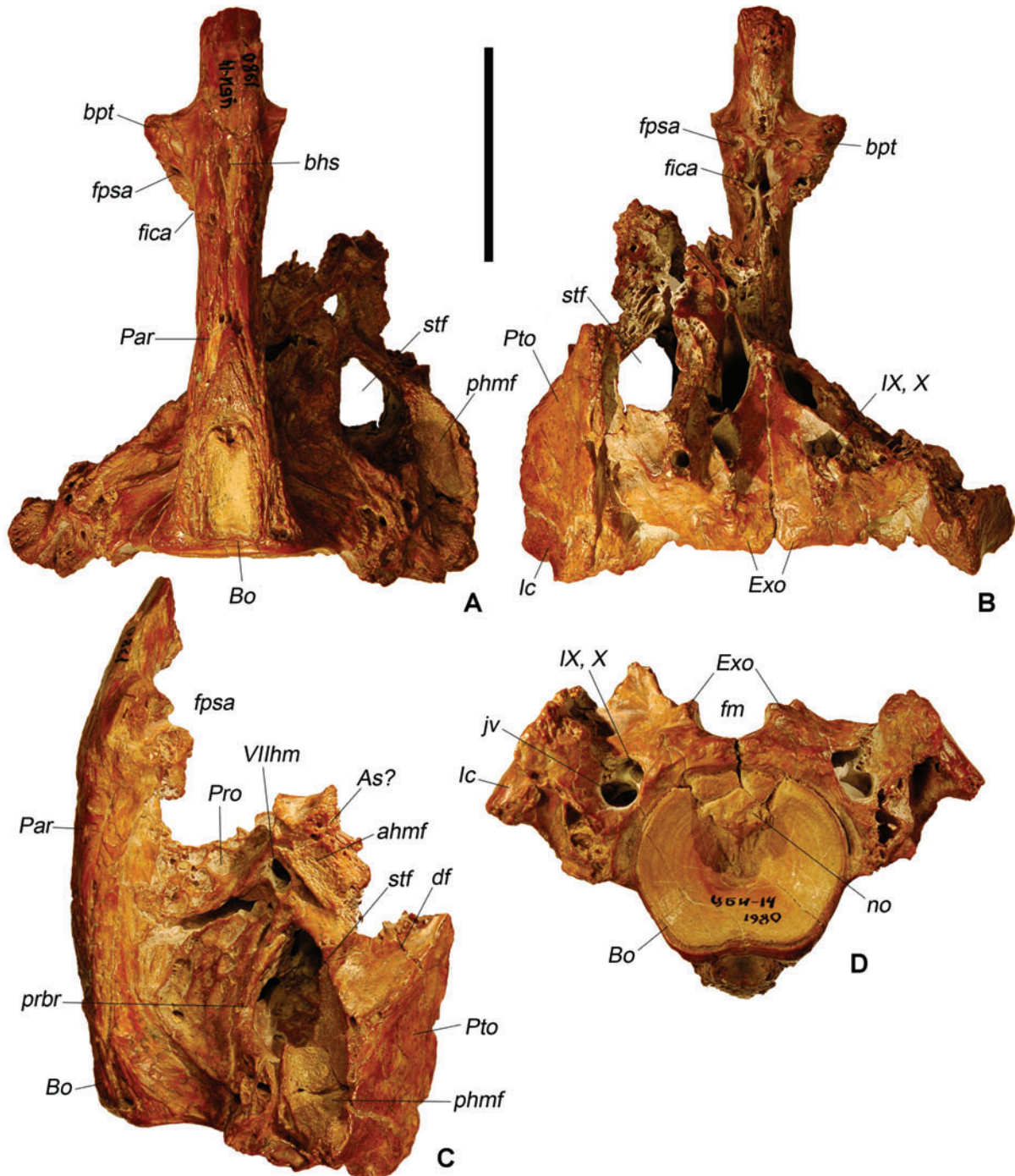
Fig. 4. *Aidachar paludalis*, partial braincase (ZIN PC 14/58), in ventral (A), dorsal (B), lateral (C), and posterior (D) views; Dzhara-kuduk, Kyzylkum Desert, Uzbekistan; Bissekty Formation, Turonian, Upper Cretaceous. *Abbreviations*: *ahmf* – anterior hyomandibular facet; *As?* – autosphenotic?; *bhs* – bucco-hypophysial slit; *Bo* – basioccipital; *bpt* – basipterygoid process; *df* – dilatator fossa; *Exo* – exoc-cipital; *fica* – foramen for internal carotid artery; *fm* – foramen magnum; *fpsa* – foramen of efferent pseudobranchial artery; *Ic* – intercalar; *jv* – jugular vein; *no* – notochord ossification; *Par* – parasphenoideum; *phmf* – posterior hyomandibular facet; *prbr* – prootic bridge; *Pro* – prootic; *Pto* – pterotic; *stf* – subtemporal fossa; *VIIhm* – foramen for hyomandibular trunk of the facial nerve; *IX, X* – common opening for glossopharyngeal and vagus cranial nerves. Scale bar = 50 mm.
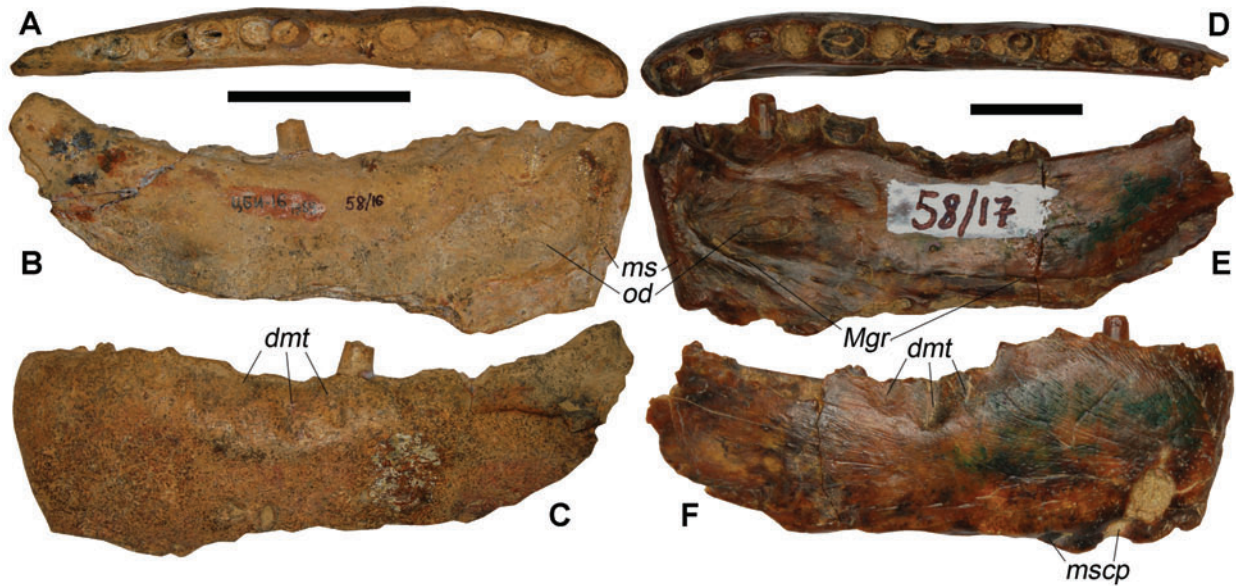
Fig. 5. *Aidachar paludalis*, left (ZIN PC 16/58, A–C) and right (ZIN PC 17/58, D–F) dentaries, in dorsal (A, D), medial (B, E), and lateral (C, F) views; Dzharakuduk, Kyzylkum Desert, Uzbekistan; Bissekty Formation, Turonian, Upper Cretaceous. *Abbreviations: dmt* – depressions for maxillary teeth; *Mgr* – Meckelian groove; *ms* – mandibular symphysis; *mscp* – pits of mandibular sensory canal; *od* – oval depression. Scale bars = 50 mm (A–C) and 10 mm (D–F).

the branches of the palatine nerve. A slit-like depression at the anterior end of this groove, between the bases of the basipterygoid processes, may correspond to the patent bucco-hypophysial canal in primitive actinopterygians (Patterson 1975).

The basioccipital forms the most part of the occipital condyle (Fig. 4D), except for the dorsal incision occupied by short exoccipital projections and a rugose bone possible representing the notochordal ossification. The occipital surface is deeply concave. In posterior view it is hexagonal, with a slightly concave ventral margin. The maximum width of the occipital condyle is 33.5 mm. Anteriorly the braincase drastically decreases in width and fuses with the prootic without a visible suture. On the ventral side of the bone, there is a wide longitudinal depression.

The dorsal surface of the exoccipitals forms the ventral floor of the foramen magnum and the cranial cavity (Fig. 4B–D). Anteroventral sides of these bones are participating in the margins of a deep subtemporal fossa. It is sutured laterally with the pterotic and intercalar, ventrally with the basioccipital, and anteriorly with the prootic. On the posterior side of the bone, between the sutures for the basioccipital, pteroticum, and intercalar, there is a large opening containing a common exit of three ca-

nals. A very small dorsal canal is separated by a thin wall from a larger dorsomedial canal. Both canals are directed anteromedially and open into the cranial cavity. These two canals are apparently for the glossopharyngeal (IX) and vagus (X) cranial nerves. The largest ventral canal is directed anteriorly and opens into the subtemporal fossa. Apparently, this canal housed the jugular vein (Patterson 1975).

The intercalar is sutured ventrally with the exoccipital and anteriorly and dorsally with the pterotic (Fig. 4B–D). The bone is exposed on the dorsal surface of the skull roof posterior to the pterotic. It forms the posterior end of the posterior facet for the hyomandibula. Apparently, at least part of the intercalar is involved in the formation of the canal for the jugular vein.

The pterotic is a large bone forming considerable part of the posterior portion of the skull roof (Fig. 4B, C). The dorsal flat of the bone forms a common flat surface with the intercalar. This surface is separated from a deepened surface of the dilatator fossa by a distinct oblique ridge. On the lateral side the dilatator fossa separates the anterior and posterior hyomandibular facets. The posterior facet is almost completely preserved on the left side. It is oval shaped and formed mostly by the pterotic.

Fig. 6. *Aidachar paludalis*, anterior fragments of left dentaries, ZIN PC 18/58 (A–C) and ZIN PC 19/58 (D–F), in dorsal (A, D), medial (B, E), and lateral (C, F) views; Dzharakuduk, Kyzylkum Desert, Uzbekistan; Bissekty Formation, Turonian, Upper Cretaceous. *Abbreviations*: *ms* – mandibular symphysis; *rt* – replacing tooth. Scale bars = 10 mm.

The prootic fuses ventrally with the parasphenoid and posteriorly with the basioccipital without a distinct suture. Along the anterior side of the prootic, there is a very deep and narrow pocket of the posterior myodome. The prootic widens dorsally where it forms a part of the ventral floor of the cranial cavity. This part of the bone is mostly damaged. On the lateral side, there is thickened prootic bridge which forms the ventral margin of the subtemporal fossa (Fig. 4C). On the lateral side, the broken bone surface reveals a subvertical canal. It is not clear if this canal is for the orbitonasal artery or posterior palatine nerve. This canal and foramen for the hyomandibular branch of the facial nerve open into a small chamber medial to the anterior hyomandibular facet and connected to the subtemporal fossa. A pair of large slit-like depressions opens into the cranial cavity near the middle line and between the exoccipitals and prootic. The anterior end of prootic is incomplete.

The piece of bone housing the anterior hyomandibular facet and a large opening for the hyomandibular branch of the facial nerve (VII) has distinct sutures with the prootic ventrally and the pterotic posteriorly, shortly before the anterior end of the posterior hyomandibular facet. It is not clear if this is still a part of the prootic or a distinct bone (autosphenotic). It forms the anterior margin of the subtemporal fossa. The anterior hyomandibular facet is incompletely

Fig. 7. *Aidachar paludalis*, isolated tooth crowns, ZIN PC 38/58 (A, B) and 39/58 (C, D), in two opposite views; Dzharakuduk, Kyzylkum Desert, Uzbekistan; Bissekty Formation, Turonian, Upper Cretaceous. Scale bar = 10 mm.
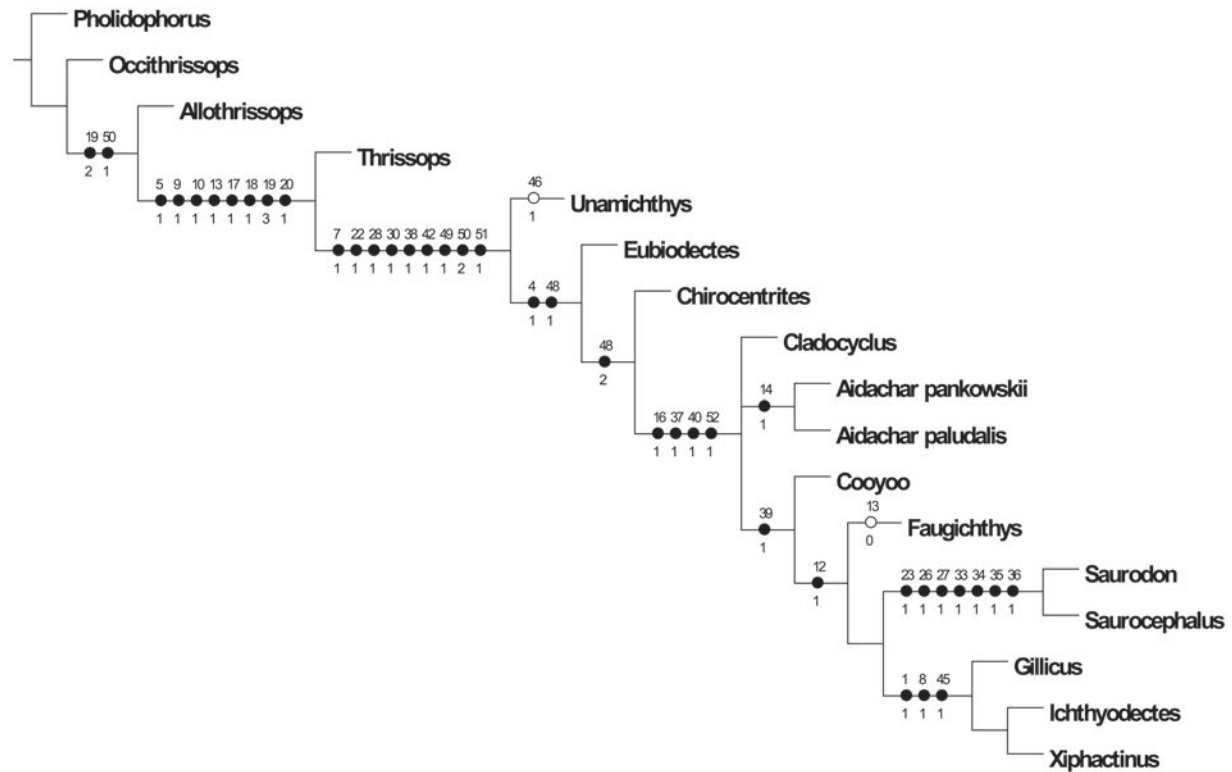
Fig. 8. Strict consensus tree of two most parsimonious trees produced by NONA 2.0 used a dataset present in Table 1. Only unambiguous characters are shown (black circles are nonhomoplasies and white circles are homoplasies). The numbers at the circles are characters (above) and states (below).

preserved. It seems likely that the whole anterior hyo-mandibular facet was formed by the autosphenotic, if this ossification represents that bone.

The dentary is represented by numerous fragments among which ZIN PC 16 and 17/58 are almost complete (Figs 5–6). The former specimen is about 3.5 times larger than the latter but the proportions of the specimens are nearly the same. The preserved length of ZIN PC 16/58 is 178 mm with the antero-posterior diameter of the largest tooth 11.2 mm. There are fragments of even larger specimens with the tooth anteroposterior diameter 17 mm (ZIN PC 28/58). The dentary is elongated bone, with the length exceeding the maximum height about three times. The alveolar border is sinusoid in lateral profile, with two convexities at the anterior and posterior ends and one middle concavity. The bone is the thickest at the alveolar border and becomes much thinner along the ventral border. Along the alveolar border within this medial concavity on the labial side there are some depressions apparently for

reception of enlarged maxillary teeth (Fig. 5). The bone is the highest at the anterior end where there is a very deep and robust mandibular symphysis (Figs 5–6). Just posterior to the symphysis on the medial side, there is a voluminous oval depression (long axis anteroposterior). In some specimens this depression could be quite deep (ZIN PC 23/58). The Meckelian groove is evident only in small specimens (Fig. 5E), where it extends from the mandibular symphysis towards the posterior end of the bone. The posterior end of the bone is upwardly curving and bears two depressions: one is along the ventral margin on the medial side and another is below the alveolar border on the labial side. The former depression is apparently for the angular. The single row of dentition extends from the mandibular symphysis for the short distance before the posterior end of the bone. There is no symphyseal diastem between the teeth of adjacent dentaries. In ZIN PC 16/58 (Fig. 5A–C) there are 17 tooth positions, 11 of which are occupied by teeth and six are alveoli (positions 4, 6, 8, 9, 15, and 17). In

ZIN PC 18/58 (Fig. 6A, B), there is a replacing tooth in the seventh tooth position before the functional large eighth tooth. The teeth are quite large, similar in length with the depth of dentary. The largest teeth are usually concentrated on the first convexity of the alveolar margin. In ZIN PC 17/58, on the lateral side along the ventral margin, two pits of the mandibular sensory canal are preserved (Fig. 5F).

The isolated teeth of *Aidachar* (Fig. 7) are quite common in the microvertebrate samples from the Bissekty Formation. They vary in length from several mm to 3–4 cm representing different tooth positions and individuals of different age. The conical tooth crowns are oval in cross section and usually bent at the apex in posterior direction. The pulp cavity extends to near the apex of the crown. In some specimens it is reduced in size and these specimens have much thicker crown walls (up to 2.5 mm in thickness). The teeth vary in the sculpturing which is not correlated with the tooth size. Some teeth are completely smooth (Fig. 7A, B), whereas others are faceted, with about a dozen of prominent ridges extending along the most of the crown except the smooth apex.

The isolated cylindrical vertebrae of *Aidachar* are similarly common at Dzharakuduk locality (e.g., Nesov 1997, pl. 3: fig. 7, pl. 6: fig. 6). The largest vertebra in the sample (ZIN PC 40/58) has the transverse diameter of 48 mm and the length of 34.5 mm. The abdominal vertebrae have closely spaced dorsal pits for the neural arch and ventral pits for the transverse processes widely separated by a flattened ventral surface. One abdominal vertebra (ZIN PC 41/58, length 12.1 mm) preserves bases of the neural arch and transverse processes. The height of abdominal vertebrae is less than its transverse diameter. On the lateral surface there are two deep slit-like depressions. The caudal vertebrae are more compressed laterally, with the height exceeding the transverse diameter.

The scales are known from few specimens (Nesov 1985, pl. 2: fig. 8; Nesov 1997, pl. 4: fig. 6). The scale is cycloid, oval-shaped (long axis vertical), with maximum thickness of about 4 mm. The largest specimens reach 78 mm in height. The scales are sculptured by concentric circles and two – four anterior radii.

PHYLOGENETIC ANALYSIS

To asses the phylogenetic position of *Aidachar paludalis* within the ichthyodectiform fishes we per-

formed a parsimony analysis based on distribution of phylogenetically significant characters discussed by Patterson and Rosen (1977), Taverne (1986), Maisey (1991), Stewart (1999), Taverne and Chanet (2000), Alvarado-Ortega (2004), and Forey and Cavin (2007). The analysis was based on the data matrix incorporating 17 taxa and 52 characters (Table 1; see Appendix for explanation of characters). All multistate characters were ordered. One thousand repetitions of the parsimony ratchet (island hopper) algorithm of NONA version 2.0 (Goloboff 1999) run with Winclada version 1.00.08 interface (Nixon 1999) produced two most parsimonious trees each with a length of 62 steps, a consistency index of 0.91, and a retention index of 0.96. The strict consensus tree is shown in Fig. 8.

DISCUSSION

The material attributed here to *Aidachar paludalis* shows five diagnostic features characteristic for ichthyodectiform fishes. One character is the synapomorphy for all ichthyodectiforms: teeth forming a single series in the jaws (character 32). The large intercalar, forming part of hyomandibular facet and enclosing a canal for the jugular vein (character 13), is a synapomorphy of all ichthyodectiforms more derived than *Allothrissops* (Fig. 8). Three remaining characters are synapomorphies for the ichthyodectiform fishes more derived than *Thrissops*. These are: deep premaxilla-maxilla attachment (character 22), deep dentary symphysis (character 28), and angled coronoid process of dentary (character 32). There is one unique character uniting *Aidachar paludalis* with *Cladocyclus pankowskii* Forey et Cavin, 2007 from the Cenomanian of Morocco: hyomandibular facet clearly divided into two parts (character 14). This character is considered here as an autapomorphy of the genus *Aidachar*, and the Moroccan species is referred here to that genus as *Aidachar pankowskii* (Forey et Cavin, 2007), comb. nov. In one of two most parsimonious tress obtained in the analysis, *Cladocyclus* is the sister taxon for *Aidachar*, in the second tree, it is sister taxon to the clade *Aidachar* + remaining ichthyodectiforms. *Aidachar* is likely related to *Cladocyclus* and, apparently, represents a vicariant taxon of the latter in the Tethys basin (Forey and Cavin 2007).

Table 1. Character matrix for phylogenetic analysis (see Appendix for the list of characters).

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                              0         1         2         3         4         5
                              1234567890123456789012345678901234567890123456789012
Pholidophorus        0?0000000000000000000000000000000000000000000000000
Occithrissops        0000000000000000000100000000000?10000000101000000000
Allothrissops        0000000000000000000200000000000010000000101000000100
Thrissops            0000100011001000113100000000000?10000000101000000100
Unamichthys          00001010110010001131?10000010111000??100111?01?0121?
Faugichthys          ???11?1011?100??????????????????????????????????????
Eubiodectes          ??011?10110010??1131?1???00101?1???0?100111????1?21?
Chirocentrites       00011010111010001131010000101?10000100111100121210
Cladocyclus          01011010111010011310100001010100001101111100121211
Cooyoo               0??11?1011?010??1131?1???0?1???1???0??11111???12121?
Aidachar pankowskii  ?101101011?01101??3?0????0011??1?000????????????????
Aidachar paludalis   ???????????110?????010??0011??10000??????????????1
Gillicus             10111111110110?11131?10?10011111000011111111?11221211
Ichthyodectes        10111111110110?11131?10??0011111000011111111?11221211
Xiphactinus          10111111110110?11131?10??0011111000011111111?11221211
Saurodon             00111110110110111311111111111111111?111111?0122121?
Saurocephalus        00111110110110111311111111111?11111?111111?0122121?
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APPENDIX. LIST OF CHARACTERS

1) Nasal: single (0), or double (1).

2) Fenestra in the dorsal aspect of the snout: absent (0), or present (1).

3) An anteriorly-directed notch (which may receive the nasal) on lateral margin of frontal: absent (0), or present (1).

4) Parietals: separate (0), or fused (1).

5) Parietals and epioccipitals located near the posterior orbital rim: absent (0), or present (1).

6) Parietals participating in supraoccipital crest: absent (0), or present (1).

7) The sensitive pit openings in the parietals lacking or reduced in number: absent (0), or present (1).

8) Anterior extend of epioccipitals: near the middle of the supraoccipital (excluding the supraoccipital crest) (0), or at the anterior end of supraoccipital (1).

9) Epioccipital crest: absent (0), or present (1).

10) High and triangular supraoccipital crest: absent (0), or present (1).

11) Large supraoccipital crest overhanging the occiput: absent (0), or present (1).

12) Pronounced reduction in the dorsal part of the supraoccipital crest: absent (0), or present (1).

13) The intercalar large and massive, forming part of the hyomandibular facet and enclosing a canal for the jugular vein: absent (0), or present (1).

14) Hyomandibular facet: common (0), or clearly divided into two parts (1).

15) Upward indentation in ventral margin of occipital condyle: absent (0), or present (1).

16) Notochordal pit divided in six sections (two paired and two unpaired, including four in the exoccipital and two on the basioccipital portion): absent (0), or present (1).

17) Basal sclerotic bone with serrate margin: absent (0), or present (1).

18) Cheek covered by large infraorbitals: absent (0), or present (1).

19) Ethmopalatine: absent (0), cartilaginous (1), partially ossified, showing cartilaginous joints (2), or completely ossified and with membranous outgrowths separating and suturing with rostrodermethmoid and lateral ethmoid (3).

20) Palatine head modified into a malleolus: absent (0), or present (1).

21) Parasphenoid-basioccipital ridges flattened: absent (0), or present (1).

22) Deep premaxilla-maxilla attachment: absent (0), or present (1).

23) Deep maxilla without a notch at rear of the palatine facet: absent (0), or present (1).

24) Sigmoid dorsal margin of the quadrate: absent (0), or present (1).

25) The quadrate head lying ahead of the orbit: absent (0), or present (1).

26) Predentary: absent (0), or present (1).

27) Enlarged dentary (terminating anterior to the premaxilla): absent (0), or present (1).

28) Dentary symphysis: shallow (0), or deep (1).

29) Angled coronoid process on dentary: absent (0), or present (1).

30) Angular contributing in the mandibular facet for the quadrate: absent (0), or present (1).

31) Retroarticular excluded from the mandibular joint: absent (0), or present (1).

32) The teeth forming a single series in the jaws: absent (0), or present (1).

33) Alveoli mostly occupied: absent (0), or present (1).

34) Teeth broad: absent (0), or present (1).

35) Teeth with carinae: absent (0), or present (1).

36) Notch or foramen at base of each tooth: absent (0), or present (1).

37) Ceratohyal with narrow fenestra: absent (0), or present (1).

38) Indented upper posterior margin of the preopercle: absent (0), or present (1).

39) Wide preopercle dorsal limb: absent (0), or present (1).

40) Large opercle: absent (0), or present (1).

41) The coracoid enlarged ventrally, meeting its fellow in a midventral: absent (0), or present (1).

42) Broad first pectoral and pelvic rays (which have a saber shape): absent (0), or present (1).

43) Short and remote dorsal fin opposed by the anal fin: absent (0), or present (1).

44) PFP ratio. The pelvic fin position or PFP is denoted as the ratio between the pectoral-pelvic fin distance (PPD) and pelvic-anal fin distance (PAD) or PFP=PPD/PAD: lower than two (0), or higher than two (1).

45) Short anal fin: absent (0), or present (1).

46) Total number of vertebrae: less than 68 (0), or 70–100 (1).

47) The first ural centrum articulation with the first two hypurals: flat (0), shallow sockets (1), or ball-and-socket articulation (2).

48) Number of epurals: three or more (0), two (1), one (2).

49) Number of uroneurals: six or seven (0), or five (1).

50) Uroneurals: do not reach the lateral surface of the preural centra (0), covering the lateral surface of the preural centra (1), or first uroneural covering the lateral surface of preural 2 or 3 (2).

51) Urodermals: present (0), or absent (1).

52) Scales: with numerous concentric circuli (0), or with anterior radii and posterior fine pitting (1).